COEXISTENCE IN A HERMIT CRAB SPECIES ENSEMBLE

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Recent studies have established that both competition and predation can be potent ecological forces in determining community diversity. However, the task of assessing the relative importance of these two forces within particular communities has barely begun. Schoener (1974) believes that studies of resource partitioning can further an understanding of the influence of competition on the diversity of ecological communities. He emphasizes that such studies must transcend the mere documentation of differences between species and consider the mechanism of competition and certain relationships between the niche parameters of the interacting species..

To keep the number of relevant niche dimensions manageable, studies of resource partitioning are usually confined to ecologically similar species within the community such as a guild or a species ensemble. A guild (Root, 1967) consists of species with similar resource exploitation patterns regardless of their taxonomic relationships. A species ensemble consists of "local, taxonomically circumscribed species assemblages" (Istock, 1973, p. 535). These categories are not mutually exclusive. For example, the members of the hermit crab species ensemble in this study are all local members of the shell-dwelling guild.

Hermit crab species ensembles are ideally suited to studies of resource exploitation because of their common guild membership. Reese (1969) first suggested the applicability of the guild concept to hermit crabs. Vance (1972) later pointed out that hermit crab guilds are appropriate for testing competition theory because much of current theory is based on the assumption that the competing species are limited by a one-dimensional resource and also because hermit crabs appeared to be primarily shell-limited. Recent studies have provided more evidence of shell-limitation (Kellogg, 1976; Spight, 1977).

The purpose of this study was to determine if partitioning of the shell resource could explain the coexistence of seven species of hermit crabs in Beaufort (N. C.) Harbor.

MATERIALS AND METHODS

Sampling procedure

During August and September, 1970, samples for shell utilization data were obtained by dredging with a 40 cm beam scallop dredge in Bulkhead Channel adjacent to the Duke University Marine Laboratory. Each dredge sample was sorted immediately after collection and each hermit crab and empty shell was placed in a compartment of a plastic tackle box. The crabs and shells were trans-

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ported to the laboratory where they were identified and measured. The sampling area and procedure are described in more detail elsewhere (Kellogg, 1971).

Shell selection

Subsequent to the previous collections, specimens of *P. longicarpus* and *P. annulipes* were collected from the study area for behavioral experiments. These crabs were held in running seawater tanks, on a natural light schedule, and fed scraps of fish or shrimp. They were exchanged for fresh specimens at weekly intervals.

To determine the preferred shell species, crabs were removed from their shells with an electric soldering gun. The anterior shield length was then measured to the nearest 0.1 mm using the ocular micrometer of a dissecting microscope. Each crab was placed in a bowl containing two shells of different species, both of which were of the preferred size for the crab. Shell width was measured to the nearest 0.1 mm by vernier caliper. The preferred shell width had been determined in previous experiments (Kellogg, 1976). The bowls (250 ml stacking type) contained 1 cm of sand and were placed in a running seawater table. After 24 hours the crab's chosen shell species was recorded. The preference rank order was determined for the four shell species inhabited most frequently by *P. longicarpus* and for the three shell species most frequented by *P. annulipes*. To avoid trying all possible combinations of shell species, it was assumed that if species A were preferred to species B, and B were preferred to C, then species A would also be preferred to species C. This made it possible to determine the preference order of *P. longicarpus* for four shell species with only four shell pairings. A shell preference order of *P. annulipes* for three shell species was determined with two shell pairings (Table III).

This method was chosen in preference to the approach taken by several other investigators (Vance, 1972; Mitchell, 1975; Grant and Ulmer, 1974) to insure that a crab's choice was based on shell morphology rather than on shell size. When species preference is determined by allowing crabs to choose from an assortment of shells similar to that found in the field, some shell species may be unrepresented over a part of their size range. This could induce crabs to select less preferred species (morphologies) to obtain more suitable shell sizes.

Shell fighting

A test for interspecific dominance in shell fighting was conducted using matched pairs of hermit crabs of different species but of the same size. One member of the pair was given a shell of preferred size, the other was given a shell 20% smaller than preferred. Crab size matching was based on the anterior shield length which was measured to the nearest 0.1 mm using the ocular micrometer of a dissecting microscope. Shell size matching was based on shell width (Kellogg, 1976) which was measured to the nearest 0.1 mm with a vernier caliper. Crabs were allowed to enter their assigned shells before placement of the pairs in 20 cm diameter stacking bowls containing 2 cm of sand and 7 cm of sea water. After 24 hours the species inhabiting the shell of preferred size was recorded to determine if a shell swap had occurred. The crab pairs tested were male *P. annulipes*/female *P. longicarpus* and *P. longicarpus*/*P. pollicaris* (both sexes). These pairings were chosen because

they represent the groups which overlap the most in their shell size use. Seventeen and twenty trials, respectively, were conducted for each of the species pairs. Approximately equal numbers of trials were begun with each of the species occupying the preferred shell to start.

Habitat selection

P. *longicarpus* and P. *annulipes* are the most common species in the subtidal regions of the estuaries near Beaufort. P. *longicarpus* occurs on a wide variety of substrates but P. *annulipes* occurs primarily in the shelly sand of the deep tidal channels (personal observation). A substrate selection experiment was conducted to determine if this distribution was due to a preference for a shell substrate by P. *annulipes*. Sand was collected from the intertidal zone near the Duke Marine Laboratory dock, and a 3 cm layer of this sand was placed on the bottom of a running seawater tank measuring 68 cm by 120 cm. Ten to fifteen pieces of broken pelecypod shell freshly collected from Beaufort Harbor Channel were placed in two opposing quadrants of the tank. The other two quadrants were left with just sand. Ten crabs of each species were placed in the tank for each of three trials. The number of crabs of each species found in each quadrant after 24 hours was recorded. The number of crabs in physical contact with the shell material and the number of crabs burrowed in the sand was also recorded.

<center>RESULTS</center>

Shell size exploitation

The shell size niches of the species inhabiting Beaufort Harbor are shown in Figure 1. The crab species are arranged on the abcissa in order of decreasing mean shell size. The major features of this comparison are that both the ratio between the mean sizes of species adjacent on the size scale (r) and the variance in the shell size inhabited by each species increase with increasing mean shell size. These trends are most clearly indicated by P. *annulipes*, P. *longicarpus*, and P. *pollicaris* which are the most abundant organisms in this collection and are most widely distributed in the Beaufort Harbor area (personal observation). P. *brevidactylus* and *Petrochirus diogenes* are relatively rare inshore and showed relatively minor departures from the values for P. *annulipes* and P. *longicarpus*. Their contribution to the trend might best be described as suggestive.

Shell size overlap between species adjacent on the size scale tends to decrease with increasing shell size (Table I). The highest overlap was for P. *annulipes*/ P. *brevidactylus*, and the lowest was for P. *pollicaris/Petrochirus diogenes*. The overlap between the two most abundant species (P. *annulipes/P. longicarpus*) was also high. Although they are not strictly adjacent on the size scale, this comparison is justified by the rarity of the intervening species (P. *brevidactlylus*). Overlap was measured by

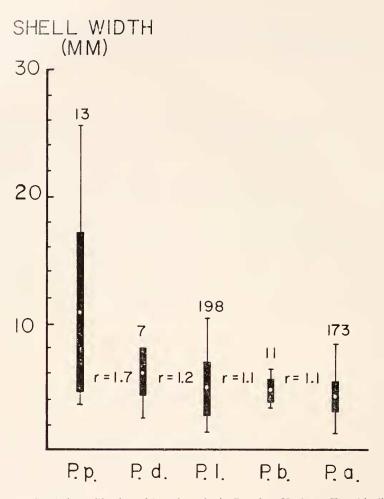$$D = 1 - \tfrac{1}{2} \sum_{i=1}^{n} |Px,i - Py,i|$$

SHELL WIDTH (MM)

FIGURE 1. Shell size utilization of hermit crabs in Beaufort Harbor. The thin lines show the range, the thick lines show one standard deviation above and below the mean. The ratios of adjacent means (r) are shown between the appropriate species. The number of individuals of each species is given above each line. Species names on the abcissa are abbreviated: P.p., *Pagurus pollicaris;* P.d., *Petrochirus diogenes;* P.l., *Pagurus longicarpus;* P.b., *Pagurus brevidactylus;* and P.a., *Pagurus annulipes.*

where Px,i is the proportion of crab species x inhabiting shell species i and Py,i is the proportion of crab species y that inhabits shell species i. One millimeter size classes were used to calculate overlap.

Shell species exploitation

Each crab species inhabits many species of shells (Table II) but tends to frequent several of them far more than the others. Two shell species comprise more than 50% of the shells utilized by each crab species. By this criterion, the crabs

TABLE I

Species names are abbreviated as in Figure 1 and are ranked in order of increasing mean size. Asterisks indicate species pairs which are adjacent on the size scale.

Species pair	Shell size overlap	Shell species overlap
P.a./P.b.*	0.80	0.74
P.a./P.l.	0.70	0.65
P.a./P.d.	0.37	0.17
P.a./P.p.	0.27	0.30
P.b./P.l.*	0.26	0.47
P.b./P.d.	0.23	0.18
P.b./P.p.	0.32	0.15
P.l./P.d.*	0.39	0.24
P.l./P.p.	0.37	0.33
P.d./P.p.*	0.23	0.66

fall into three shell specialization groups: first, *P. annulipes* and *P. brevidactylus* specialize in *Anachis avara* and *Nassarius vibex*; secondly, *P. longicarpus* specializes in *N. obsoletus* and *N. vibex*; and thirdly, *P. diogenes* and *P. pollicaris* specialize in *Polinices duplicatus* and *Terebra dislocata*.

The differences in shell species inhabitation may be explained partly on the basis of size differences. *P. duplicatus* is one of the few shells large enough for the sexually mature females of the third group. Ovigerous females of the smallest species, *P. annulipes* and *P. brevidactlylus*, are found most frequently in *Anachis avara* shells, the largest of which is too small for reproductively mature individuals of all the other species. Reproductively mature *P. longicarpus* females are found most

TABLE II

Shell species utilized by hermit crabs in Beaufort Harbor. The number of shells inhabited by each crab species is tabulated. Crab species names are abbreviated as in Figure 1.

Shell species	P.a.	P.b.	P.l.	P.d.	P.p.
*Anachis avara**	61	4	16	—	—
A. translirata	6	2	7	—	—
Epitonium sp.	2	—	—	—	—
Eupleura caudata	8	—	8	—	—
Fasciolaria hunteri	2	—	1	—	1
Mitrella lunata	2	—	2	—	—
Nassarius obsoletus	12	—	60	1	1
N. trivittatus	—	—	2	—	—
N. vibex	37	2	57	—	—
Olivella mutica	5	—	5	—	—
Polinices duplicatus	—	—	2	3	6
Terebra dislocata	18	2	18	3	2
T. concava	3	—	—	—	—
Urosalpinx cinerea	12	1	16	—	—
Worm tube	2	—	—	—	—
Other species**	5	—	4	—	3

* See Morris (1973) for gastropod taxonomic authorities.
** Number of species which were represented by only one individual.

frequently in *N. vibex* and *N. obsoletus* shells which are larger than those required by females of the first group and smaller than those required by mature females of third group.

Shell morphology also influences the shell species inhabitation, since differences in shell species inhabitation of *P. longicarpus* and *P. annulipes* exist even within size classes. Shell species overlap within the 1.0–1.4 mm and 1.5–1.9 mm crab size classes is 0.64 and 0.65, respectively. Overlap within the largest size class which contains both *P. longicarpus* and *P. annulipes* (2.0–2.4 mm) is only 0.51. Shell species overlap values were calculated using the formula described above for shell size overlap.

Shell species preference

P. longicarpus, in this experiment, demonstrated a strong shell morphology preference in all of the choices except one (Table III). There was only a weak preference for *N. obsoletus* over *L. irrorata.* The preference order for *P. longicarpus* is therefore *N. vibex* > *N. obsoletus* ≥ *L. irrorata* > *T. dislocata.* *P. annulipes,* in this experiment, clearly preferred *A. avara* to *N. vibex* and *N. vibex* to *N. obsoletus.*

Shell fighting

No evidence of interspecific dominance was found among the three most abundant species of this ensemble. No shell swaps occurred in any of the trials, despite the fact that the crabs were allowed to interact for 24 to 48 hours. Possibly a different stress would have elicited fighting. For example, Hazlett (1970) showed that hermit crabs in larger shells rap harder when fighting and this increases their likelihood of evicting an opponent. Therefore, had one crab of the pair been given a preferred shell and the other a shell larger than preferred, the stressed crab might have been more successful. In nature, however, inhabiting a small shell is the more common and more stressful condition for hermit crabs (Vance, 1972; Kellogg, 1976). Interspecific shell fighting is apparently not the cause of the observed shell resource partitioning.

TABLE III

Shell species preference of P. longicarpus *and* P. annulipes. *The probabilities are for the two-tailed binomial test.*

Hermit crab species	Shell species	Numbers chosen	Probability
Pagurus longicarpus	*N. vibex/N. obsoletus*	17/3	0.0026
P. longicarpus	*N. obsoletus/L. irrorata*	14/6	0.1153
P. longicarpus	*N. obsoletus/T. dislocata*	19/1	0.0004
P. longicarpus	*L. irrorata/T. dislocata*	20/0	<0.0001
P. annulipes	*A. avara/N. vibex*	9/1	0.0059
P. annulipes	*N. vibex/N. obsoletus*	10/0	0.0020

Substrate selection

P. *annulipes*, in this experiment, demonstrated a distinct preference for a shelly substrate by selecting the quadrats having shell fragments more often than those with just sand ($P = 0.004$; two-tailed binomial test). P. *longicarpus* showed no preference for either sandy or shelly substrates. The affinity of P. *annulipes* for shell material was further demonstrated by the observation that 11 of the thirty specimens were in direct contact with shell fragments, compared to only 4 of the thirty P. *longicarpus*. Eleven of the thirty P. *annulipes* were burrowed in the sand at the conclusion of the experiment, as compared to only one P. *longicarpus*. The crabs burrowed in the sand so that their shells were covered but their eyestalks, legs, and antennae protruded. Their antennae were swept forward over the sediment surface periodically in an apparent feeding motion. P. *annulipes* has setose antennae which may trap food particles carried along the sediment surface by tidal currents. P. *longicarpus* lacks such setae and feeds instead by traveling over the substrate and tossing debris into its mouth parts with its minor cheliped (Roberts, 1968). In the estuary, P. *longicarpus* is found on a wide variety of sediments (*e.g.*, sand, mud, shelly sand), but P. *annulipes* is generally restricted to the shelly, sand substrate of the tidal channels (personal observation). The differences in the distribution of these two species are due at least in part to their differing substrate preference and to their differing feeding styles.

DISCUSSION

Schoener (1974) proposes that regular spacing of niches along a single dimension be accepted as evidence of resource partioning generated by competition. He notes that size ratios of adjacent species are typically 1.2 or higher and that in some cases there is a tendency for ratios to increase as sizes increase. The ratios between adjacent species in this ensemble increase from 1.1 to 1.7 as the utilized resource size increases. This indicates that competition and consequent resource partitioning is more pronounced for the larger species. This interpretation is supported by the observation that large empty shells are scarcer than small ones in this area (Kellogg, 1976).

Shell size partitioning seems to be the most important factor permitting coexistence of at least the largest three species in this ensemble, *i.e.*, *Pagurus longicarpus*, *Pagurus pollicaris*, and *Petrochirus diogenes*. Competition for shells is most severe for these species, and size ratios for adjacent species are in the range reported as the typical degree of size separation for a variety of other organisms in direct competition (Schoener, 1974). Although shell species overlap was also low for these species, this is due mostly to the size differences so shell species partitioning cannot be considered of great importance here. In other locations, many specimens of *Pagurus pollicaris* were collected within the size range of *Pagurus longicarpus*, and their shell species utilizations were similar (personal observation).

The presence of *Petrochirus diogenes* in this ensemble is somewhat puzzling because, although it inhabits shells of relatively large size, no sexually mature individuals were collected either here or in other estuarine collections. Offshore, however, much larger specimens of *Petrochirus diogenes* were collected (even larger

than the largest *Pagurus pollicaris*), many of which were sexually mature. This suggests that *Petrochirus diogenes* does not maintain a viable breeding population in this area, but that stray larvae may drift into the estuary from offshore. Some of them apparently locate unused shells which occur in the channels. Shells inhabited by *Petrochirus diogenes* usually were heavily fouled, unlike those found in other areas, and unlike those inhabited by the other species (personal observation). *Petrochirus diogenes* does not prefer shells in this condition. When placed in holding tanks containing a wide variety of shells (conditions, sizes, and species), the *Petrochirus diogenes* specimens readily abandoned their orginal shells for clean ones. The survival of *Petrochirus diogenes* in this area may be attributed to errors of exploitation (Istock, 1973) by *P. longicarpus* and *P. pollicaris* and to partitioning of the shell size spectrum.

Several specimens of two other species, slightly smaller than the mean size of *Petrochirus diogenes,* were also collected in the study area but were not included in the analysis because of insufficient numbers. Both of these species are abundant in certain offshore locations. *Paguristes hummi* was found in *T. dislocata* (the shell least favored by *Pagurus longicarpus*). *Pagurus impressus,* which is similar in morphology to *Pagurus pollicaris* and attains the maximum size of *P. pollicaris* offshore, was collected in this study area, but only as relatively small individuals. *Pagurus impressus* and *Paguristes hummi* can find some small, unexploited shells, but not enough of the appropriate size to sustain a breeding population here.

Shell size partitioning by the smaller species (*Pagurus annulipes, Pagurus brevidactylus,* and *Pagurus longicarpus*) seems less important to their coexistence than for the others. However, it is not negligible. *P. annulipes* and *P. brevidactylus* are very similar in the sizes and species of shells used. They are also very similar in appearance and behavior. There is no apparent difference in their shell use or behavior which can explain their coexistence, assuming that they in fact compete for shells. *P. brevidactylus,* however, is rare in this area but abundant offshore on rocky substrates with a dense fouling community (personal observation). The presence of large pieces of shell covered with a dense fouling community in this area provides an adequate, albeit restricted, substrate for this species in Beaufort Harbor. The existence of *P. brevidactylus* in this area may be due to the presence of shell debris and the availability of a very limited supply of shells not used by *P. annulipes* and *P. longicarpus* (i.e., errors of exploitation). Perhaps the most complex competitive relationship is that between *P. annulipes* and *P. longicarpus.* They are the most abundant species in this study area and are also similar in size and shell species utilization. If *P. brevidactylus* is disregarded because of its relative rarity and *P. annulipes* and *P. longicarpus* are considered as adjacent species on the size scale, we find that they have a size ratio of 1.2, which is within the range suggested by Schoener (1974) as the minimum size separation necessary for the coexistence of competing species along a resource gradient.

In addition to the size differences, shell species utilization differences between *P. annulipes* and *P. longicarpus* are significant. This is shown by the relatively low niche overlap between the two species within the 2.0–2.4 mm size class, which includes mostly reproductively mature individuals of both species.

Schoener (1974) notes that increasing ratios of species sizes are correlated with an increased variance in the food size utilizations of larger species. He states that

the variances of food sizes should generally be greater for larger species for two reasons. First, large food items are usually scarcer than small ones and secondly, large species usually have a wider size range. The higher variance, he believes, would cause more overlap (hence more competition) between larger species and would necessitate wider niche spacing.

The trend toward higher variance in shell size utilization for the larger species in this ensemble is accompanied by both of these conditions. First, large shells are relatively scarce (see above) and secondly, the first crab stages of all species are similar so that the size range of species increases in proportion to maximum size.

However, rather than the expected higher shell size overlap with increased crab size, the reverse trend was observed. The greatest overlap was between the smallest species ($P.a./P.b.$), and the least overlap was between the largest species ($P.d./P.p.$). Presumably, overlap among the largest species has been reduced by competitive interactions in the past.

Complementarity of overlap values for two independent niche dimensions can also indicate resource partitioning (Schoener, 1974). For example, hermit crabs with a high size overlap would be expected to overlap less in other dimensions (*e.g.*, shell species) if they are resource limited. Most of the species in this ensemble had an overlap value of less than 0.50 for one or both niche dimensions (shell size and shell species). Only the smaller species ($P.a./P.b.$, $P.b./P.l.$, and $P.a./P.b.$) had high overlap values for both niche dimensions. Furthermore, shell species overlap was greatest between the smaller size classes of *P. annulipes* and *P. longicarpus*. This lack of complementarity among the smaller crabs demonstrates that shell resource partitioning is less crucial to their coexistence than it is for the larger ones.

Shell size partitioning is apparently maintained by differences in growth potential and size at sexual maturity which are evolutionary adaptations to a long history of competition. Partitioning seems not to result from interspecific exclusion by shell fighting, because crabs were not induced to swap shells in laboratory experiments. Nor does it arise from habitat differences in shell size, because both *P. longicarpus* and *P. pollicaris* frequent the same habitats. Furthermore *P. annulipes*, the smallest crab species, does not use large shells such as *Busycon* spp. and *Fasciolaria hunteri*, although these snails inhabit the study area.

Shell species (morphology) partitioning is maintained in part by differences in crab morphology and shell preference. *P. annulipes*, for example, prefers *Anachis avara* shells which are elongate and have a small aperture height relative to the shell width (Kellogg, 1971). Fecund female specimens of *P. annulipes* and *P. brevidactlyus* were most often found in these shells. Female specimens of *P. annulipes* and *P. brevidactlyus* have smaller chelipeds for a given crab weight than males; their chelipeds are also smaller than those of both male and female *P. longicarpus* and *P. pollicaris*. This enables them to use shells with a more restricted aperture, such as *Anachis avara* or *Terebra dislocata*, more effectively. *P. longicarpus*, in contrast, shuns the elongate, heavy, small-apertured *T. dislocata*. Unfortunately, suitable sizes of *T. dislocata* were unavailable when shell preference for *P. annulipes* was determined, but *T. dislocata* would probably rank higher in the preference order of *P. annulipes* than it did for *P. longicarpus*. The suggestion

that *P. annulipes* makes more effective use of *T. dislocata* than *P. longicarpus* is supported by the observation that in subsequent sampling offshore, where most of the shells were *T. dislocata,* specimens of *P. annulipes* were predominant.

Habitat differences also help explain shell species partitioning. For example, *N. obsoletus* shells are available to individuals of *P. longicarpus* and *P. pollicaris* because these crabs often forage in the intertidal zone to which *N. obsoletus* is restricted. Individuals of *P. longicarpus* often overturn live *N. obsoletus,* inspect the shell aperture, and then release them, apparently in search of an empty shell or dead snail (personal observation). In contrast, *P. annulipes* individuals were never observed in the intertidal zone. *P. annulipes* is most abundant in the channels along with large numbers of *Anachis avara* which inhabits the fouling community attached to shell debris.

In order of decreasing importance, habitat differences, shell size partitioning, and shell species partitioning maintain the diversity of this species ensemble. Probably only three species (*P. annulipes, P. longicarpus,* and *P. pollicaris*) could coexist in this area if the surrounding areas were homogeneous with the study area, forcing the crabs to rely only on subdivision of the shell resource for ecological differentiation. The presence of the other species in this area is apparently sustained by breeding populations elsewhere, by errors of exploitation of those breeding here, and by the relatively large number of small empty shells.

Among other studies of hermit crab species ensembles, as in this study, it appears that differences in shell size utilization and habitat are most important in allowing coexistence. Grant and Ulmer (1974, p. 40) note that "a large proportion of the *P. acadianus* population exceeds the size range of *P. pubescens*" within their study areas in Maine. They found, however, that the shell species utilization of these crabs was similar within size classes. Vance (1972) has studied shell use in the *P. hirsutiusculus, P. granosimanus, P. beringanus* ensemble in the Pacific intertidal. He found that although *P. hirsutiusculus* preferred shorter, lighter shells than the others, the differences in shell utilization between the three species in the field were slight and not sufficient to explain their coexistence. He did find, however, a marked habitat difference among them which he concluded was the primary reason for their coexistence considering the extensive overlap in shell use. Bollay (1964) studied another group of sympatric hermit crabs of the Pacific intertidal (*P. hirsutiusculus, P. granosimanus,* and *P. samuelis*). She noted that *P. hirsutiusculus* was smaller than the other species and that both *P. hirsutiusculus* and *P. samuelis* attained sexual maturity at a smaller size than did *P. granosimanus.* Furthermore, she found that where *Tegula funebralis,* the largest shell species, was scarce, *P. hirsutiusculus* was relatively abundant, *P. samuelis* was scarce, and *P. granosimanus* was absent. This strongly suggests partitioning of the shell size range although this relationship was not quantified. Samuelson (1970) reports distinct differences in the size range of the four hermit crab species in a subtidal ensemble in Norway. *Anapagurus chiroacanthus* is the smallest of the four, *P. cuanensis* and *P. prideauxii* are intermediate in size, and *P. bernhardus* attains the greatest size. *P. prideauxii* inhabits relatively small shells for its size because of a symbiotic anemone which attaches to its shell. The anemone grows as the crab grows, thus obviating the need to find larger shells. This suggests that shells have been scarce in the past thereby creating evolutionary pressure which caused some species to use other means of protection.

Summary

The shell exploitation of hermit crabs inhabiting a subtidal region of Beaufort Harbor (N. C.) was studied to determine the importance of shell resource partitioning in allowing the coexistence of the hermit crabs. The three most abundant species (*Pagurus annulipes, P. longicarpus,* and *P. pollicaris*) partition the size range. The size ratio between the larger species (*P. pollicaris* and *P. longicarpus*) was 1.7 and the size ratio between the smaller species (*P. annulipes* and *P. longicarpus*) was only 1.2. Differences in shell species utilization were significant only for the smaller species (*P. annulipes* and *P. longicarpus*). Specimens of four other hermit crab species were collected (*Pagurus brevidactylus, Pagurus impressus, Paguristes hummi,* and *Petrochirus diogenes*). Individuals of these species are more prevalent offshore. In Beaufort Harbor they use relatively small shells or shells which tend to be overlooked or shunned by the other species.

Experiments on shell selection, interspecific fighting, and substrate selection were conducted to determine the mechanism by which habitat differences and shell resource partitioning are maintained. Differences in shell preference and substrate preference were found between *P. longicarpus* and *P. annulipes*. However, no interspecific shell fighting dominance was observed for *P. longicarpus, P. annulipes,* and *P. pollicaris*.

Coexistence of individuals of the seven species of hermit crabs collected in Beaufort Harbor is made possible by a combination of habitat differences, shell size partitioning, and shell species partitioning in descending order of importance. The shell partitioning of the three most abundant species is maintained by differences in maximum crab size at sexual maturity, and by differences in shell species preference. Habitat differences between *P. annulipes* and *P. longicarpus* are maintained in part by a preference for shell debris by *P. annulipes*.

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